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Brandvain, Y., A.M. Kenney, L. Flagel, G. Coop, and A.L. Sweigart. Submitted on 26 Oct 2013. Speciation and introgression between *Mimulus nasutus* and *Mimulus guttatus*. arXiv:1310.7131v1 [q-bio.PE].

The study by Brandvain et al., published online via arXiv, presents "**a population genomic investigation of the speciation history of two closely related species of monkeyflowers,**" ... "the first population genomic analysis of *Mimulus guttatus* and *M. nasutus*." It is based on the results of whole genome analyses of *M. guttatus* (13 populations), *M. nasutus* (5 populations), and *M. dentilobus* (1 population, as an outgroup) through sampling that "spanned the ecological and geographic ranges of each species." "We use these dense and contiguous population genomic data to estimate the population-split time, quantify rapid loss of ancestral variation accompanying the transition to selfing in *M. nasutus*, and identify ongoing, bidirectional introgression. Additionally, we observe a negative correlation between the recombination rate and interspecific divergence between *M. nasutus* and sympatric *M. guttatus*, a result best explained by selection against introgression of *M. nasutus* ancestry. Our approach provides a detailed view of differentiation and introgression in a tractable ecological, genetic, and evolutionary model system."

**ABSTRACT** "*Mimulus guttatus* and *M. nasutus* are an evolutionary and ecological model sister species pair differentiated by ecology, mating system, and partial reproductive isolation. Despite extensive research on this system, the history of divergence and differentiation in this sister pair is unclear. We present and analyze a novel population genomic data set which shows that *M. nasutus* ``budded'' off of a central Californian *M. guttatus* population within the last 200 to 500 thousand years. In this time, the *M. nasutus* genome has accrued numerous genomic signatures of the transition to predominant selfing. Despite clear biological differentiation, we document ongoing, bidirectional introgression. We observe a negative relationship between the recombination rate and divergence between *M. nasutus* and sympatric *M. guttatus* samples, suggesting that selection acts against *M. nasutus* ancestry in *M. guttatus*."

The techniques and technology that allow these data to be gathered are remarkable and the neighbor-joining tree (NJTree) with congruent PCA provide interesting insights. Much of the interpretation and inference, however (especially that with phrases like "suggesting," "likely reflecting," "likely due to," "hinted at," "presumably as," and "it seems"), incorporates confused and unfounded assumptions and circular reasoning, and coupled with lack of documentation and limited sampling, it gives little confidence that associated interpretations coincide with what actually is happening in the evolution of these plants.

In a more precise taxonomic context, names for the species discussed here would be positioned in the genus *Erythranthe*, one of the segregates established by Barker et al. (2012) among the species of *Mimulus* sensu lato. In the comments here, however, plants are identified as *Mimulus* rather than *Erythranthe* (some newly described species do not have a name in *Mimulus*), not because of ambivalence regarding their taxonomic placement but instead for ease of comparison with the Brandvain et al. discussion.

**Lack of documentation**

The remarkable convention in the Brandvain et al. study, following that of many other molecular-genetic investigations, in not providing vouchers for the samples means that analyses cannot be objectively interpreted or independently evaluated. They can be repeated only by using exactly the same samples, not by anyone wishing to make an independent attempt toward the same observations. Even from a molecular-genetics outsider's point of view, it is hardly what one expects from mainstream science.

**Confused assumptions**

The outgroup from Arizona is identified as *Mimulus dentilobus*, but that species is endemic to northwestern Mexico (Nesom 2012) — the Arizona species closely related to *M. dentilobus* (and mostly identified as *M. dentilobus* prior to 2012) is *M. parvulus*, which presumably accurately identifies the outgroup. Not that this affects the outcome of the study, but generally it is useful and desirable to be accurate as possible, and the correct identification could have been made simply by reference to maps in Nesom (2012). Further, choice of *M. dentilobus* as the outgroup in the Brandvain et al. study was arbitrary. Even though little is securely known of the internal phyletic structure of sect. *Simiolus*, a potentially more informative choice of outgroup might have been made from a species of the Decora group or Tilingii group (Nesom 2012), both of which are primarily centered in the same region as species in the study (the Guttata and Microphylla groups) and probably more closely related to them. The *M. dentilobus* group is highly specialized, has a base chromosome number of x = 16 (vs. x = 14 in *M. guttatus* and its close relatives), and is primarily from Mexico.

More significantly, all other populations in the study are identified as *Mimulus nasutus* or *M. guttatus*. *Mimulus nasutus* is clearly a closely coherent species morphologically and genetically but it can be inferred from Brandvain et al.'s Table S1 that at least two other species are represented among the remaining 13 samples — rhizomatous *M. guttatus* is distinct from annual *M. guttatus*, the latter better identified as *M. microphyllus* (Nesom 2012, 2013b). In addition to these two, three other species are tentatively identified here among the 13. Alternative identifications are offered in the following paragraphs, as summarized in Figure 2. Of the 13 *M. guttatus* samples, AHGT, BOG, CAC, DPR, DUN, IM, LMC, MAR, REM, SLP, SWB, and YJS represent populations that have been used in previous studies or that are currently being used (e.g., Sweigart & Willis 2003; Lowry et al. 2008; Sweigart et al. 2008; John Willis, pers. comm. 2013); PED and YJS are listed in Seed Collections (2009).

North group

CACG (Klickitat Co., Washington) is characterized in Brandvain et al.'s Table S1 as an annual and identified here as *Mimulus microphyllus*. The IM (Linn Co., Oregon) and MAR (Douglas Co., Oregon) samples also are *M. microphyllus*, the annual. The NJTree-paired BOG (Humboldt Co., Nevada) and YJS (Lehmi Co., Idaho) are perennial and evidently are appropriately identified as rhizomatous *M. guttatus* sensu stricto.

The AHQT sample (Park Co., Wyoming) represents a population from thermal soil in Yellowstone National Park. All *Mimulus guttatus* except AHQT in that region is rhizomatous — the locale is far west of the range of annual *M. microphyllus*. Lekberg et al. (2012) reported that the AHQT population differs from non-thermal populations of the same immediate area in its lack of rhizomes, smaller size, denser vestiture, phenology (flowering begins earlier in the season), and floral biology/mating system (AHQT is autogamous). AHQT also is genetically distinct (as studied from 7 microsatellite and gene-based nuclear markers) and genetically isolated from all other populations in the area. These observations provide prima facie evidence for regarding AHQT as a distinct morphological and biological species — this is exactly the set of evidence usually called for and accepted in such an assessment — and indeed these plants were named as a species in 1900, as *Mimulus thermalis* A. Nelson. I accepted this taxonomic assessment and rank (Nesom 2012), noting that *M. thermalis* is the only known example of sympatric speciation in *Erythranthe*. It also appears to be a bonafide example of what Brandvain et al. refer to as speciation by "budding off" (see below, Speciation history). In Figure 2, AHQT is identified as "guttatus s. str. > thermalis," recognizing its direct evolutionary connection to rhizomatous *E. guttatus*.

South group

A sample from southeastern Arizona (PED, mapped apparently from Cochise County, from "San Pedro River" fide Seed Collections 2009) is sister to all other samples of the South group in the NJTree and is correspondingly isolated in the PCA. It might represent an introgressed population of rhizomatous *Mimulus guttatus* or perhaps it is the annual *M. unimaculatus* (duration of PED was noted as "?" in Table S1). *Mimulus cordatus* (Subgroup C/D of the Microphylla group, Nesom 2012) is common in Cochise County, and although it produces autogamous flowers I have encountered many collections of *M. cordatus* that were originally identified as *M. guttatus*. Plants of *M. cordatus* are fibrous-rooted annuals, but larger plants of the species characteristically produce leafy, rhizome-like runners from basal nodes and root from proximal nodes of the stems. Because PED is isolated in the analyses from *M. guttatus* samples, and because *M. cordatus* is relatively common in southeastern Arizona, I have identified PED as the latter. Of course, while this ID is plausible it is speculative — PED may well represent rhizomatous *M. guttatus*, in which case the sample still would be accomodated by the arrangement in Figure 1. At least it contributes to a point made here, that identifications by the authors are ambiguous at best.

DUN (Lane Co., Oregon) and SWB (Mendocino Co., California) are *M. grandis*, as inferred from their use in previous molecular-genetic studies (e.g., Lowry et al. 2008). LMC (Mendocino Co., California) and REM (Napa/Lake Co., California) comprise a pair sister to *M. grandis* in the neighbor-joining analysis; each is characterized as annual; REM is from serpentine. Their identity, judging from the disposition of LMC in Lowry et al. (2008), is *M. microphyllus*, but their close alliance with *M. grandis* is unexpected because of the much closer morphological similarity of *M. grandis* and rhizomatous *M. guttatus*.

In the Brandvain et al. analysis, the NJTree sister to *Mimulus nasutus* is the DPRG-SLP group (both samples from Tuolumne Co., California). Both DPRG and SLP are characterized as annual; SLP is specifically noted in Table S1 to be from a serpentine habitat (from the Red Hills, fide John Willis, pers. comm.). The type collection of *M. pardalis* was made in 1919 from the serpentine Red Hills of Tuolumne County and, based on the information (or lack of it) presented by Brandvain et al., it would be possible that the DPRG-SLP group represents *M. pardalis*, which is among the species suggested (Nesom 2012) to be most closely related to *M. nasutus*. I am assured, however (John Willis, pers. comm.), that the DPRG-SLP plants are among those that would be identified as *M. microphyllus*.

It is only slightly tangential here to note that *Mimulus pardalis* has often been identified as *M. guttatus*. Macnair postulated that a new species, which he described as *Mimulus cupriphilus*, had been derived within the last 50 to 150 years directly from annual *M. guttatus* (= *M. microphyllus*) at the site of a California copper mine — it was later pointed out (Nesom 2012) that the putative new species has a much wider distribution, more characteristically occurs on serpentine, and had been named as *M. pardalis* more than 40 years earlier. Wright et al. (2013) discussed the increase in frequency of a hybrid incompatibility allele in a copper-substrate population at the site earlier studied by Macnair — they identified the copper-tolerant plants in the study simply as *M. guttatus*, not indicating whether they were *M. pardalis* (a.k.a. *M. cupriphilus*, which is not even mentioned in the paper) or Macnair's hypothesized "parental" *M. guttatus*. According to John Willis (pers. comm.), they are appropriately identified as *M. microphyllus*.

Focal samples

Among the 4 focal samples ("sequenced to high depth," "high depth, high quality") of *Mimulus guttatus* used in the PSMC analysis, AHQT is immediately derived from rhizomatous *M. guttatus*. DPRG and SLP are identified here (from information not included in any publication) as *M. microphyllus*. Each of these three apparently is a widely divergent variant within the broad population the authors apparently intended to study. The fourth sample, CACG, presumably also is correctly identified as *M. microphyllus*.

**Unfounded assumptions**

Brandvain et al. observe that "*Mimulus guttatus* and *M. nasutus* are an evolutionary and ecological model sister species pair differentiated by ecology, mating system, and partial reproductive isolation." Evidence for their characterization as either kind of "sister species pair" (evolutionary, ecological) is neither presented nor discussed in the text and thus their pairing, especially their evolutionary pairing, appears to be an assumption upon which the study is based. An "evolutionary species pair" or a "sister species pair" typically indicates that the two taxa are immediately derived from the same ancestor, that they are each other's closest relative. Evidence in support of this would exist as a well-supported phylogenetic hypothesis for the species comprising *Mimulus* sect. *Simiolus*, at least for a significantly inclusive group of sect. *Simiolus* species pertinent to the considerations in the study. I am not aware that any such evidence exists. A hypothesis that at least provides an adequate taxonomic framework is an infrasectional classification, which I noted to be "admittedly subjective," laid out in the recent taxonomic study of sect. *Simiolus* (Nesom 2012). Figure 1 is a hypothetical cladistic depiction of that classification — it is one among many possible topologies that would have to be refuted before a plausible claim could be made regarding a evolutionary sister relationship between *M. microphyllus* and *M. nasutus*.

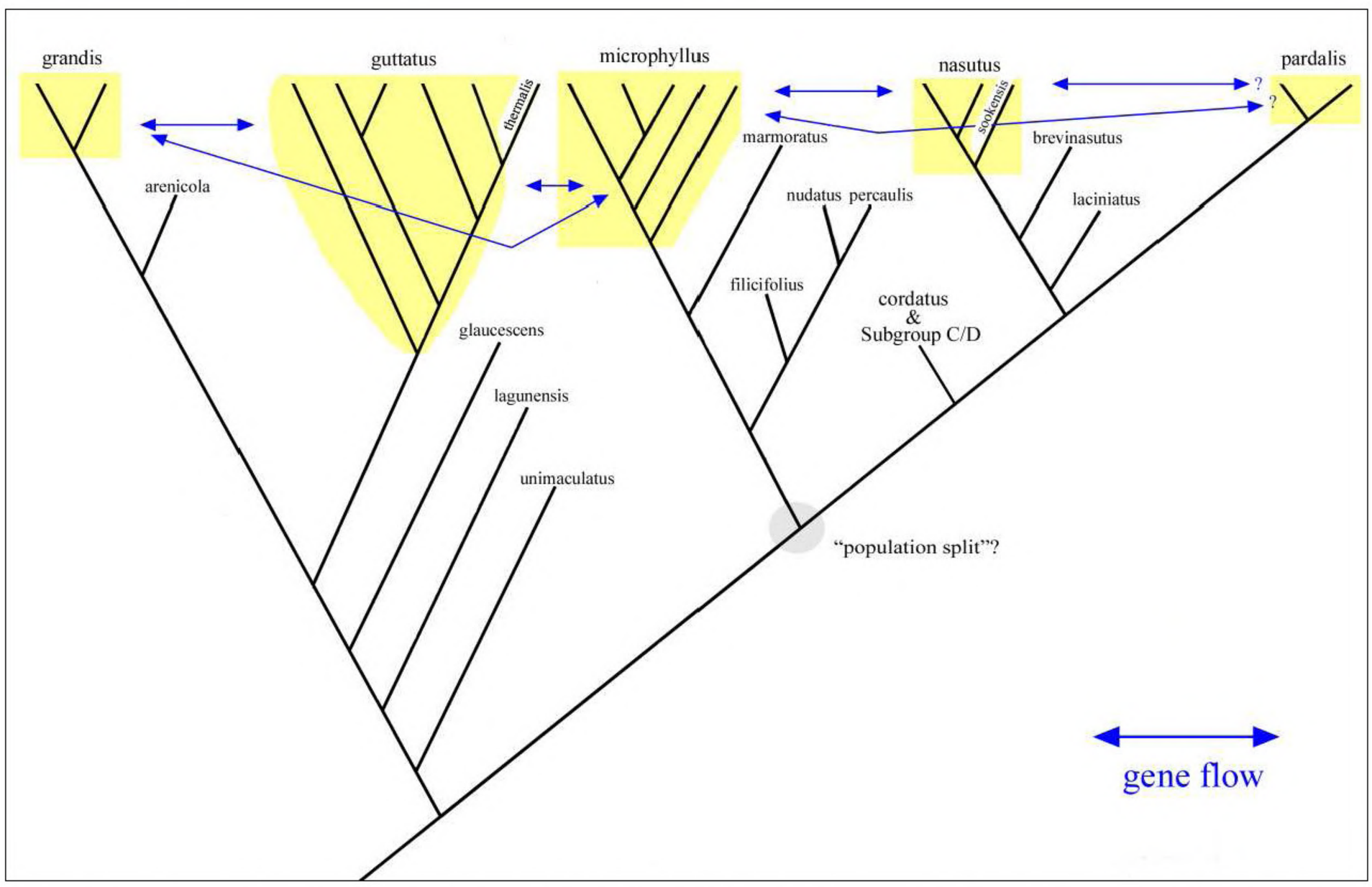


Figure 1. Hypothetical phylogeny of part of sect. *Simiolus*. *Mimulus grandis*, *M. guttatus*, *M. microphyllus*, *M. nasutus*, and probably *M. pardalis* each comprise populations that are characterized by portions of genome of other species (the origin of these "outside" genes attributed here to common ancestry and introgression), and some populations within each species may be reproductively isolated. Each, however, apparently has an ancestral coherence that allows all populations to be recognized as a single species (a morphological species), as indicated by the yellow highlight; selective processes also may impose ecological and morphological constraints. *Mimulus thermalis* has been derived from a population of *M. guttatus*. *Mimulus sookensis* is hypothesized to be of hybrid origin between *M. nasutus* and *M. microphyllus*, but it is morphologically identical to *M. nasutus* and thus included here within *M. nasutus* considered as a morphological species.

In that informal classification and the derivative phylogram (Fig. 1), closest relatives of *Mimulus nasutus* are hypothesized to be *Erythranthe brevinasuta*, *M. laciniatus*, and *M. pardalis*. These all are annual with autogamous flowers, basal and proximal cauline leaves often purplish, and flowers often produced at all nodes, proximal to distal. It was noted that this group is perhaps arbitrarily separated from the group that includes *M. microphyllus* as well as *M. glaucescens*, *M. marmoratus*, and *M. nudatus*, and now with recent descriptions (Sexton et al. 2013; Nesom 2013d, 2013e), also *Mimulus filicifolius* and *Erythranthe percaulis* — all these also are annual but have generally larger flowers that are allogamous. Because the Brandvain et al. study also includes plants characterized as perennnial (rhizomatous), a phylogenetic hypothesis to identify sister relationships also would necessarily include *M. guttatus* in the strict sense (which is rhizomatous) and species hypothesized to be most closely related to it — *M. grandis*, *M. arenicola*, *M. thermalis*, *M. unimaculatus*, and *Erythranthe lagunensis*.

The PED sample clusters with the NJTree South group — PED is identified here as *Mimulus cordatus* (Subgroup C of the Microphylla group, which also includes M. *arvensis*, *M. brachystylis*, and *M. charlestonensis*; Nesom 2012). *Mimulus hallii* first was separated as Microphylla Subgroup D but it is better placed with the species of Subgroup C, which together constitute a group where diversification through vicariant speciation is a reasonable hypothesis (see Maps 15 and 16 in Nesom 2012; Map 5 in Nesom 2013c).

In sum, there is no basis for an a priori assumption that *Mimulus guttatus* (in any sense except a "multi-species," one that includes 4 or 5 or more separate species) is the sister species of *M. nasutus*. Results of the Brandvain et al. analysis itself might allow the possibility that such is the case (the neighbor-joining sister to *M. nasutus* is DPRG-SLP = *M. microphyllus*), but the clustering pattern of a NJTree does not necessarily correspond to the cladistic history (see comments below). And, obviously, the sister to *M. nasutus* in the analysis can only be found among the samples included — there are other possibilities, unconsidered.

**Circular reasoning, speciation history, transition to selfing**

*Mimulus guttatus* and *M. nasutus* are assumed to be sister species, and then the study includes only *M. guttatus* and *M. nasutus* among the samples — the conclusion that one is derived from the other, or that they have an immediate common ancestor, is inescapable. This reasoning and its associated presumptions/conclusions, which underlie the whole study, dilute the meaning of the discussion.

Speciation history

The whole study is characterized as "an investigation of the speciation history" of *Mimulus nasutus* and *M. guttatus*. The authors find that "Genetically, *M. nasutus* clusters with central Californian *M. guttatus* samples, suggesting that speciation post-dated the differentiation of some *M. guttatus* populations. Thus, speciation in this pair is best described as a 'budding off' of *M. nasutus* from *M. guttatus*, rather than a split of an ancestral species into two." And (p. 3) "overall patterns of genomic differentiation show deep population structure in *M. guttatus*, with *M. nasutus* diverging from a central Californian *M. guttatus* population approximately 200 kya. … The fact that *M. guttatus* is paraphyletic (i.e., split by *M. nasutus*) suggests that *M. nasutus* budded from within a structural ancestral *M. guttatus* population." In view of the circular reasoning and the non-cladistic nature of a neighbor-joining tree, and with the problems in incomplete geographic and taxonomic sampling and identification of samples, such interpretations of speciation vary from ambiguous to meaningless. Inferences of the "population-split time" may be objective, but if *M. microphyllus* is not sister to *M. nasutus*, then perhaps the estimates are of the earliest time when their separate clades diverged from a common ancestor (see Fig. 1).

Transition to selfing

It is implied (if not intended to be unequivocally stated) that *Mimulus nasutus* acquired its self-pollination syndrome as part of the process of speciation in which it was derived from outcrossing *M. guttatus* (i.e., "The evolutionary transition from outcrossing to self-fertilization, as occurred in *M. nasutus* ..." (p. 2); "The transition from outcrossing to self-fertilization in *M. nasutus* has had clear consequences on patterns of genomic variation." (p. 10); "We observe an approximate coincidence between the timing of divergence and the decline in population size in *M. nasutus* (as inferred from our PSMC analysis), likely as a result of the transition to selfing being linked to speciation." (p. 10). The evolutionary polarity of the transition in pollination biology is based on a reasonable assumption, derived from observations in many other plant groups, that the autogamy is derived from an allogamous ancestral state, but without unequivocal evidence regarding the events of speciation, the ancestral allogamy and origin of autogamy, including its timing, in *M. nasutus* can only be speculative.

Although flowers of rhizomatous *Mimulus guttatus* and *M. microphyllus* are consistently allogamous and herkogamous, corolla size and anther/stigma arrangement in both species are variable and it is not implausible that a small-flowered population might become autogamous (e.g., as in *M. thermalis*). The distinctive morphology of *M. nasutus* (vestiture, stem shape, leaf shape, inflorescence configuration, calyx shape and coloration), however, makes it difficult to accept that it was immediately derived from *M. microphyllus*. Based on the hypothesis that the closest relatives of *M. nasutus* are *Erythranthe brevinasuta*, *M. laciniatus*, and *M. pardalis* (Nesom 2012, p. 14; Fig. 1), all autogamous annuals, a reasonable correlate was noted to be that "The suite of characters associated with autogamous fertility is heritable" — an autogamous species could be ancestral to other autogamous species. This is almost certainly the case in Subgroup C/D of the Microphylla group (all autogamous annuals), although in this instance geographic disjunctions apparently underlie a pattern of vicariant speciation. *Mimulus nasutus* and *E. brevinasuta* probably are evolutionary vicariants; *M. nasutus* is at least currently sympatric with both *M. laciniatus* and *M. pardalis*.

**Limited sampling — ecological and geographic ranges**

The claim that collection of samples "spanned the ecological and geographic ranges of each species" (p. 3) appears not to be centrally significant to the intent of the study, because neither the ecological nor geographical parameters of that claim are matched by the samples.

* The southernmost sample of *Mimulus nasutus* is from central California. The species occurs southward into Baja California and southeastward through Arizona into New Mexico. Essentially the only area where it is not sympatric with *M. microphyllus* is Arizona and New Mexico (see maps in Nesom 2013a).

* The southernmost sample of annual *Mimulus guttatus* (*M. microphyllus*) is from central California; the northernmost sample is from southern Washington. The species ranges into southwestern British Columbia and southward to the southern counties of California. Essentially the only areas where it is not sympatric with *M. nasutus* are southern British Columbia and northern Baja California (see maps in Nesom 2013a).

* The only samples of rhizomatous/perennial *Mimulus guttatus* (excluding the two samples of *M. grandis*) are from Idaho and Nevada. Rhizomatous *M. guttatus* (*M. guttatus* sensu stricto) is widespread over the western USA, into Mexico (Baja California, Sonora, Chihuahua), and through western Canada into Alaska (Nesom 2012, 2013c). A locality from the Queen Charlotte Islands mapped on Brandvain et al.'s Figure 1A does not appear among the samples and does not figure in the analysis — the only plants of sect. *Simiolus* in the QCI are rhizomatous *M. guttatus*.

Given the broad morphological and geographic diversity within rhizomatous *Mimulus guttatus* and other species as well, the limited sampling leaves open many possibilities in interpretation of the speciation history of this group. Conclusions of the analysis can only be based on the samples included. Unsampled taxa and geographically divergent populations might prove to be interpolated among the branches of the NJTree, requiring changes in interpretation.

**Neighbor-joining tree with revised identifications**

The topology of the Brandvain et al. neighbor-joining tree (their Figure 1B) is reproduced here as Figure 2, with original sample names substituted by species names based on surmises discussed above. If the Figure 2 revision is at all a closer approach to biological realities than the generalized identifications in 1B, presumably this would alter the study's interpretations and discussion. Without vouchers, however, there is no way of determining correct identities (nor could there be basis for a claim that the original Figure 1B is more appropriate than the revised Figure 2).

A prominent feature reflected in the NJTree is the intermixing of *Mimulus microphyllus* samples among those of other species. In the South group, portions of the genome are shared between *M. microphyllus* and *M. nasutus* and between *M. microphyllus* and *M. grandis*. In the North group, portions of the genome are shared between *M. microphyllus* and rhizomatous *M. guttatus*.

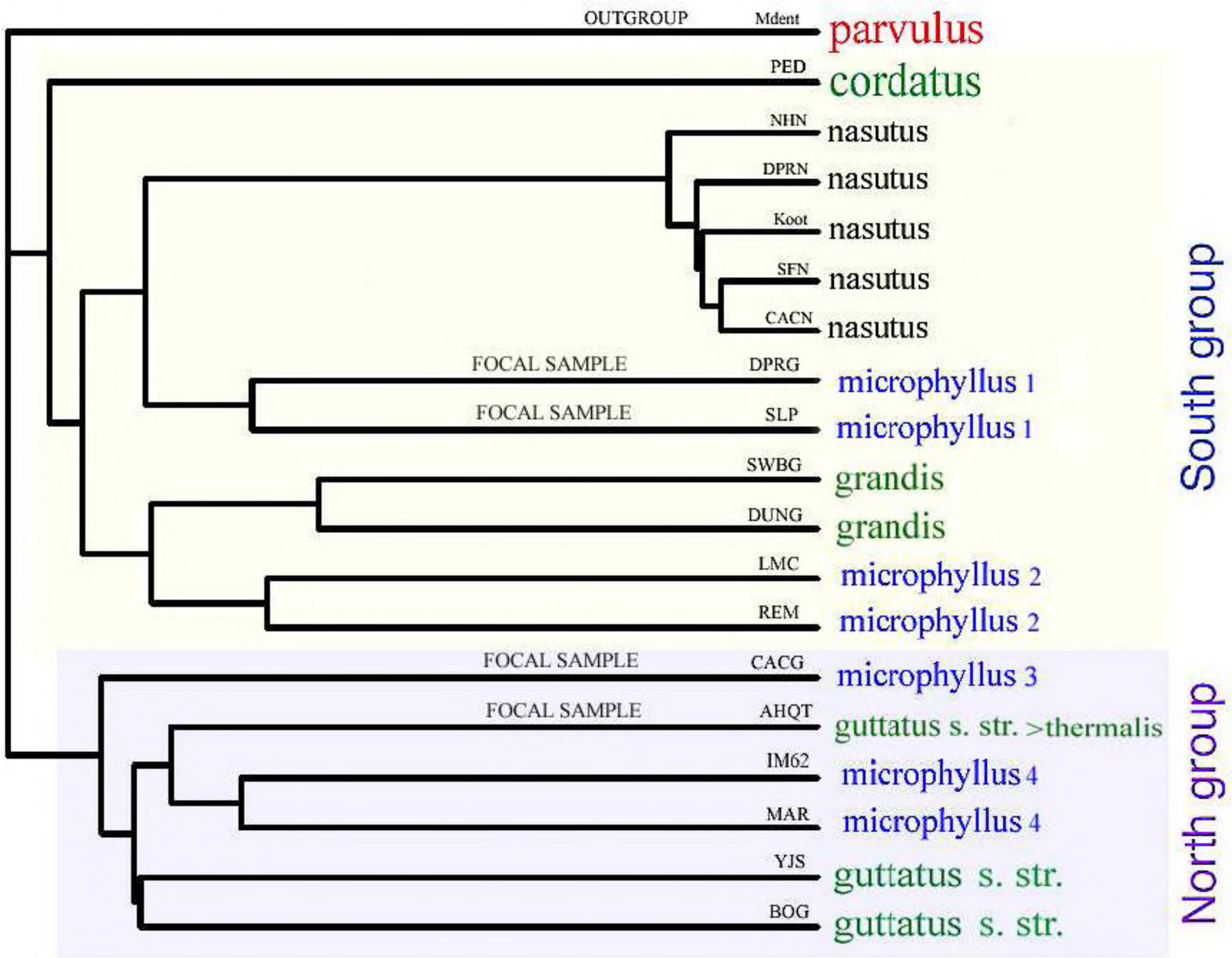


Figure 2. Neighbor-joining tree topology of Figure 1B of Brandvain et al., with hypothetical alternative identifications of the samples (see comments in text). The original sample codes are shown to the left in smaller font. The new names are hypothetical since without vouchers there is no way of making objective identifications.

*Mimulus microphyllus* as I have identified it might appear to be non-monophyletic in the NJTree, comprising several independent lineages (Brandvain et al. note [p. 3] that *M. guttatus* is "paraphyletic" in their analysis). I have suggested earlier that evolutionarily independent lineages of rhizomatous *M. guttatus* might also be found, but the sampling here does not allow that to be tested.

*Mimulus grandis* (rhizomatous, perennial) in the NJTree clusters with samples of annual *M. microphyllus* rather than rhizomatous *M. guttatus*. It was earlier observed that annual duration in sect. *Simiolus* may be plesiomorphic, which would not be inconsistent with independent evolution of rhizome production in *M. guttatus* and *M. grandis* — "Rhizome production in *Erythranthe* occurs in scattered species and species groups and may be derived in each of the instances. In sect. *Simiola*, rhizomes are produced in about half of the species and those species may all have arisen from annual, non-rhizomatous ancestors" (Nesom 2012, p. 9). Brandvain et al. note (p. 3) that the NJTree "clearly displays a deep phylogenetic split within *M. guttatus*, roughly corresponding to northern and southern parts of its range." The separate positions of rhizomatous *M. guttatus* and *M. grandis* in the North and South groups might be taken to confirm their evolutionary independence, in spite of their morphological similarity. On the other hand, the distance between *M. guttatus* and *M. grandis* shown in the NJTree may reflect introgression in parallel rather than a cladistic disparity.

Various comments throughout the discussion directly imply that the authors interpret the NJTree as a cladogram, but neighbor-joining produces an arrangement based on phenetic similarities (distance measures), not one intended to be interpreted as a cladistic topology. It might be argued that the large amount of genetic data adduced in whole genome studies, even when interpreted with a neighbor-joining algorithm, produces an arrangement of samples similar to a phylogenetic analysis, but this is speculative. In the present study, a cladistic interpretation of the NJTree seems so implausible to me (compare Figure 1) that the NJTree groupings are more reasonably interpreted as reflective of gene flow than a pattern of phylogeny.

## LITERATURE CITED

Barker, W.R., G.L. Nesom, P.M. Beardsley, and N.S. Fraga. 2012. A taxonomic conspectus of Phrymaceae: A narrowed circumscription for *Mimulus,* new and resurrected genera, and new names and combinations. Phytoneuron 2012-39: 1–60.

Benedict, B.G., J.L. Modliszewski, A.L. Sweigart, N.H. Martin, F.R. Ganders, and J.H. Willis. 2012. *Mimulus sookensis* (Phrymaceae), a new allotetraploid species derived from *Mimulus guttatus* and *Mimulus nasutus*. Madroño 59: 29–43.

Lekberg, Y., B. Roskilly, M.F. Hendrick, C.A. Zabinski, C.M. Barr, and L. Fishman. 2012. Phenotypic and genetic differentiation among yellow monkeyflower populations from thermal and non-thermal soils in Yellowstone National Park. Oecologia 170: 111–122.

Lowry, D.B., R.C. Rockwood, and J.H. Willis. 2008. Ecological reproductive isolation of coast and inland races of *Mimulus guttatus*. Evolution. 62: 2196–2214.

Nesom, G.L. 2012. Taxonomy of *Erythranthe* sect. *Simiola* (Phrymaceae) in the USA and Mexico. Phytoneuron 2012-40: 1–123.

Nesom, G.L. 2013a. The taxonomic status of *Mimulus sookensis* (Phrymaceae) and comments on related aspects of biology in species of *Erythranthe*. Phytoneuron 2013-69: 1–18.

Nesom, G.L. 2013b. Observations on habit and duration in populations of *Erythranthe microphylla* and *E. guttata* (Phrymaceae). Phytoneuron 2013-68: 1–8.

Nesom, G. L. 2013c. New distribution records for *Erythranthe* (Phrymaceae). Phytoneuron 2013-67: 1–15.

Nesom, G.L. 2013d. A new species of *Erythranthe* sect. *Simiola* (Phrymaceae) from California serpentine. Phytoneuron 2013-70: 1–6.

Nesom, G.L. 2013e. *Mimulus filicifolius* joins *Erythranthe* (Phrymaceae). Phytoneuron 2013-80: 1–2.

Seed Collections. 2009. Seed collections — seeds from wild populations and permanent mapping populations (last seed database update noted as 22 Mar 2009). Mimulus Community 2013. Announcements, The genus *Mimulus*, *Mimulus* genome, people, seed collections, techniques. OpenWetWare. <http://openwetware.org/wiki/Mimulus_Community>

Sexton, J.P., K.G. Ferris, and S.E. Schoenig. 2013. The fern-leaved monkeyflower (Phrymaceae), a new species from the northern Sierra Nevada of California. Madroño 60: 236–242.

Sweigart, A.L. and J.H. Willis. 2003. Patterns of nucleotide diversity are affected by mating system and asymmetric introgression in two species of *Mimulus*. Evolution 57: 2490–2506.

Sweigart, A.L., N.H. Martin, and J.H. Willis. 2008. Patterns of nucleotide variation and reproductive isolation between a *Mimulus* allotetraploid and its progenitor species. Molec. Ecol. 17: 2089–2100.

Wright, K.M., D. Lloyd, D.B. Lowry, M.R. Macnair, and J.H. Willis. 2013. Indirect evolution of hybrid lethality due to linkage with selected locus in *Mimulus guttatus*. PLoS Biol 11(2): e1001497. doi:10.1371/journal.pbio.1001497

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